

# The Pallial Ridge of *Neotrigonia*: Functional Siphons Without Mantle Fusion

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(1 Plate, 2 Text figures)

## Mantle Fusion and Bivalve Evolution

FROM RELATIVELY MODEST beginnings in Ordovician times (POJETA, 1971), the Bivalvia have steadily increased in diversity to become a dominant element of the modern benthos. Almost all the earliest bivalves were sluggish and shallow burrowing, infaunal suspension feeders. The absence of mantle fusion precluded very active or deep burrowing; for without fusion, true siphons could not be formed. Moreover, the most efficient modern burrowers (TRUEMAN, 1966) use ventral fusion to perfect their hydraulic mechanism (STANLEY, 1968:221). Among the advantages of ventral fusion are rapid extrusion of the foot (by valve adduction with siphons closed) and the direction of a more powerful stream of water anterior to the foot before each sequence of pedal contraction (to loosen sediment for easier penetration of the shell).

In an excellent series of papers, STANLEY (1968, 1970, 1972) has traced the spectacular success of the Bivalvia to a pair of distinctive adaptations that extended the original, shallow infaunal habitat to new ecological realms. 1) Bivalves became important members of the epifauna by neotenus retention of the byssal attachment that characterizes only the early post-larval stages of most burrowing forms (STANLEY, 1972; YONGE, 1962). 2) The evolution of mantle fusion permitted development of siphons and resultant colonization of deeper infaunal habitats by more rapid and efficient burrowers. Of the two events, STANLEY (1968) emphasizes the second as the major determinant of the great Mesozoic-Cenozoic radiation of the bivalves (15 new superfamilies, all siphonate and most eulamellibranch heterodont).

The original state of shallow infaunal life without mantle fusion is still retained by some groups usually regarded as "primitive." These taxa are often highly successful and diverse—some nuculoids and arcoids in par-

ticular (YONGE, 1957:154). Yet, among this group, is a phyletic remnant, a coelacanth among bivalves. The Australian *Neotrigonia* is the only surviving genus of a dominant Mesozoic group. The entire Tertiary record of the Trigonidae is confined to two genera in Australia, New Zealand and New Guinea (FLEMING, 1964; GOULD, 1968; SKWARKO, 1967).

The mantle edges of *Neotrigonia* are completely unfused (except, of course, dorsally at the mantle isthmus with slight extension recorded in a short ligamental fusion layer). *Neotrigonia* lives in the "original" bivalve habitat—infaunally with the posterior margin at or just barely above the sediment surface (McALESTER, 1965; Stanley, personal communication). The strong, distinctive radial ornament probably serves to keep the shell anchored in its burrow. *Neotrigonia* lives subtidally in waters surrounding Australia and Tasmania; like most relatively inefficient, non-siphonate burrowers, it has not colonized the intertidal zone (STANLEY, 1968:223). A strong, muscular foot (GOULD, 1969), however, provides *Neotrigonia* with greater speed in burrowing than its general design would imply.

## Separation of Inhalent and Exhalent Water in *Neotrigonia*

The posterior part of the mantle has never been accurately described in *Neotrigonia*. The subject is of special interest because bivalves without mantle fusion must still develop some mechanism for separating incurrent and excurrent waters. An examination of the shells of several species, and of the soft parts of *Neotrigonia margaritacea* (dredged from the East Arm of Western Port, Victoria and kindly supplied by Drs. N. D. Newell and S. M. Stanley) led to the following results.

1. Two lots from Western Australia (Museum of Comparative Zoology, Department of Mollusks, Nos. 92155 and 251173), probably members of VERCO's (1907) taxon *Neotrigonia bednalli*, have the posterior margin of the shell divided into two lobes by a median indentation (Figure 1); dried mantle fragments adhering to the shell in Lot No. 92155 show that the indentation corresponds to the point of division between incurrent and excurrent waters. The indentation is very faint in *N. lamarckii*, and scarcely evident in the type species *N. margaritacea*.

2. The posterior papillae of the mantle edge are cleanly divided by size and complexity into excurrent and incurrent parts (Figure 2). The postero-ventral (incurrent) papillae are large and ramose; those on the postero-dorsal (excurrent) margin are small and simple, like those that continue all along the ventral border. Since incurrent waters must be freed of large debris, such differentiation is not unusual in bivalves. In *Petricola pholadiformis*, for example, large tentacles of the incurrent siphon act as strainers, while those of the exhalent siphon are much smaller (PURCHON, 1955).

3. *Neotrigonia* has evolved a structure, apparently unique among the Bivalvia, which produces functional siphons without any mantle fusion whatever. We name this structure the pallial ridge (Figures 3 and 4). The pallial ridge runs in an antero-posterior direction along the internal surface of each mantle lobe. It is located medially on the posterior margin, where the papillae of incurrent and excurrent apertures meet. When the mantle edges are applied to each other, the ridges are apposed, producing a firm division between incurrent and excurrent waters. Other bivalves with unfused mantles can

form "siphons" by local apposition (pp. 5, 6), but only *Neotrigonia* has evolved an actual structure to effect the separation. Moreover, the pallial ridge is a complex and subtly constructed organ, probably operated hydraulically by the circulatory system.

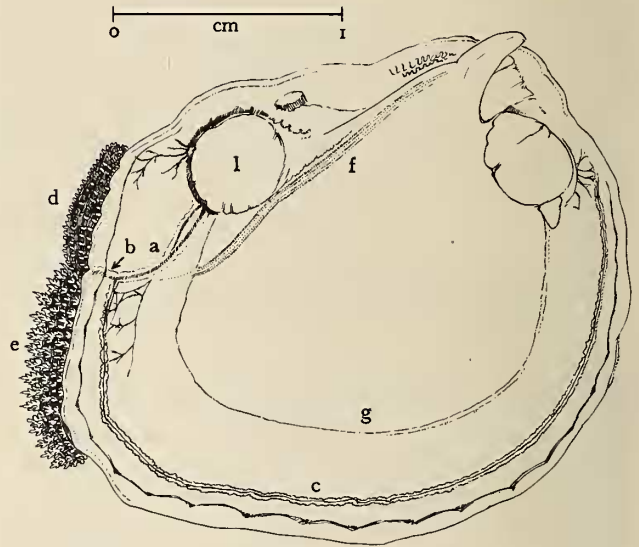


Figure 3

Detail of pallial ridge, right side, interior view  
 a - blood vessel to pallial ridge and pallial vessel; c - pallial blood vessel; d - excurrent siphon; e - incurrent siphon; f - line of attachment of mantle to shell; g - pallial line; h - spongy part of pallial ridge; i - hollow, tubular part of pallial ridge; j - posterior part of pallial ridge; k - blood vessels to edge of mantle; l - posterior adductor muscle

### Explanation of Figures 1, 2, 5, 6, and 7

Figure 1: Exterior of right valve of *Neotrigonia bednalli* from Western Australia (Museum of Comparative Zoology, Department of Mollusks, lot 251173). Actual length of specimen is 22.2 mm. Posterior indentation marking separation of incurrent and excurrent waters is indicated by a

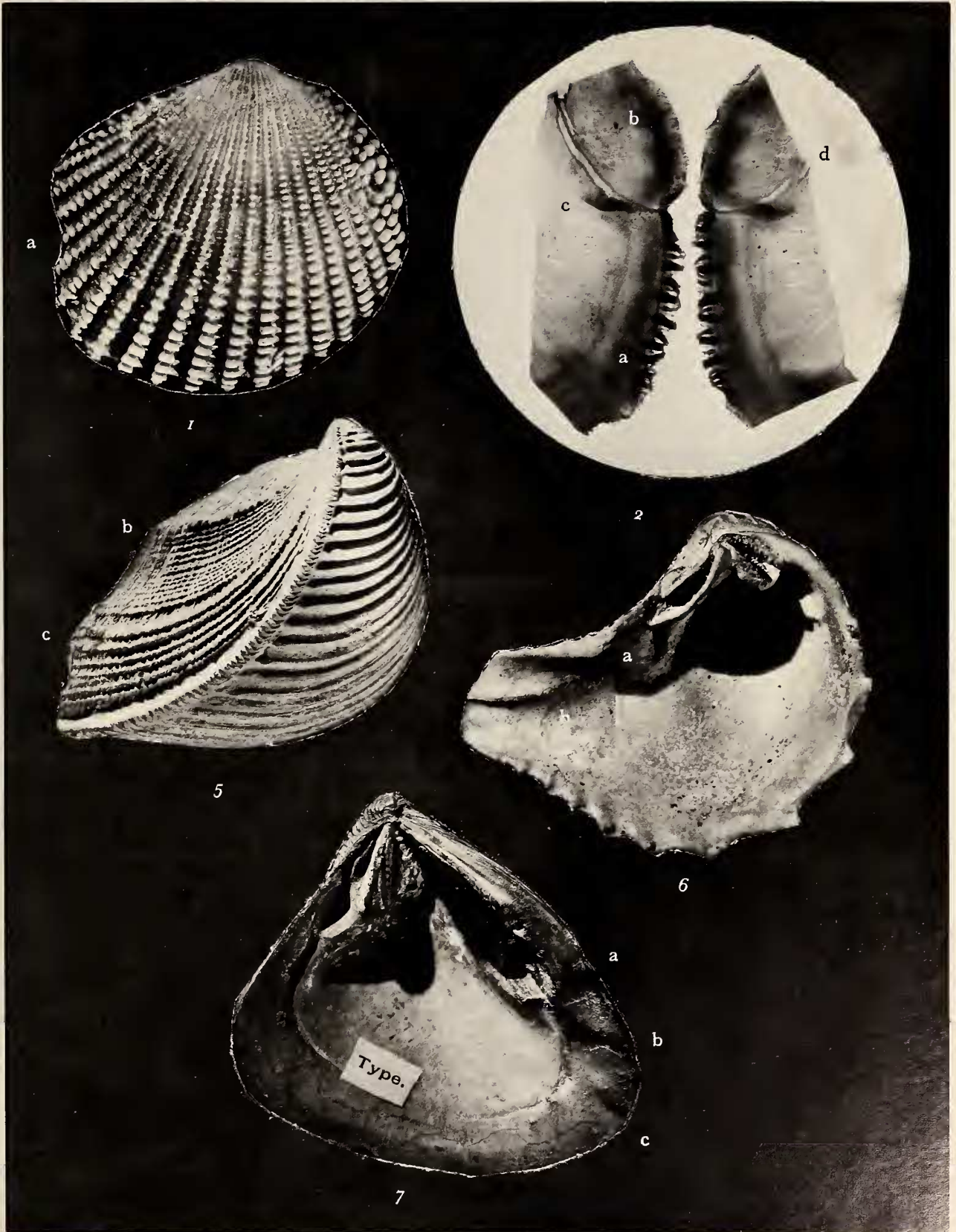
Figure 2: Interior views of posterior mantle of *Neotrigonia margaritacea*, showing mechanisms for separation of incurrent and excurrent flow. a - large, ramose incurrent papillae; b - small, simple excurrent papillae; c - pallial ridge; d - blood vessel to pallial ridge. Actual dorso-ventral length is 15.0 mm

Figure 5: A "typical" fossil (Jurassic) trigonian; external view of right valve. "*Trigonia costata*"; Department of Invertebrate Paleontology, Museum of Comparative Zoology, No. 2698. Actual length of specimen is 46.5 mm. a - marginal carina; b - escutcheon carina; c - median furrow of area marking separation of incurrent and excurrent waters

Figure 6: Internal ridges and raised areas marking paths of incurrent and excurrent flow. *Pterotrigonia eufaulensis*, Upper Cretaceous, Ripley Formation. Actual length of specimen is 31.8 mm. a - shelf corresponding to escutcheon and marking dorsal wall of excurrent flow; b - internal median ridge. Note how well excurrent flow is channeled by dorsal and ventral walls

Figure 7: Complete delimitation of incurrent and excurrent "siphons" in a fossil trigonian. Actual length of specimen is 73.9 mm. a - internal shelf corresponding to escutcheon and marking dorsal wall of excurrent flow; b - internal median ridge; c - groove corresponding to external marginal carina (an internal ridge on the left valve meets this groove and forms a ventral border for incurrent flow)







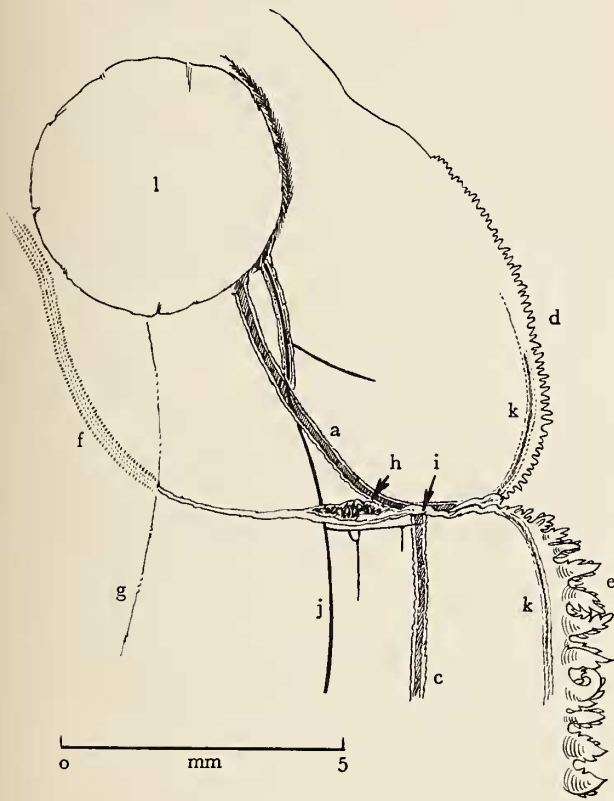


Figure 4

Right side of animal, outside view. Total length  $2\frac{1}{2}$  cm  
 a - blood vessel to pallial ridge and pallial vessel; b - position of pallial ridge; c - pallial blood vessel, with spongy walls; d - excurrent siphon with small, simple tentacles; e - incurrent siphon with large, complex tentacles; f - line of attachment of mantle to shell, running along somewhat pronounced rib inside shell; g - pallial line of mantle

The pallial ridge (Figures 3h and i) runs antero-posteriorly from the proximal edge of the muscular inner mantle lobe to the notch between the excurrent (d) and incurrent (e) "siphons." Running from the anterior end of the ridge to the top of the visceral mass is a line of attachment of the mantle to the valve (f). This line secures the proximal end of the pallial ridge in a constant position.

A blood vessel (a) from the region of the posterior aorta descends over the postero-dorsal surface of the posterior adductor muscle (l), and runs postero-ventrally beneath the posterior part of the pallial ridge (i), where it sends a major branch ventrally into the mantle (c) and lesser

branches into the tentaculate edges of the "siphons." The walls of the larger vessels are composed of spongy, porous tissue which allows blood to flow into the tissues of the mantle.

The posterior pallial nerve (j), arising from the proper visceral ganglion, descends through a blood vessel, crosses the main feeder vessel (a), and usually passes beneath the anterior end of the ridge (h). This nerve sends minor branches toward the edges of the mantle in both "siphons." The small nerve in the incurrent "siphon" usually passes just ventral to the ridge; in one specimen, this nerve followed the feeder vessel.

The ridge itself has two parts. The medial portion (h) is made of spongy tissue like that forming the walls of the larger blood vessels. This part is roughly lenticular. Covering this part, and extending anteriorly to the pallial line (g) is a thin ridge of translucent, tough tissue. Posterior to the spongy tissue, and continuous with the translucent tissue is a tube (i). This tube runs to the ventral edge of the excurrent "siphon."

The ridge may operate in this way: blood from the feeder vessel (a) passes into the spongy part of the ridge (h). It then passes, perhaps under the influence of variable permeability, into the posterior tubular portion of the ridge (i), and possibly into the narrow, anterior ridge. During feeding, the pallial ridge might thus be distended with blood to effect a better separation of currents; it may be collapsed when the shell is closed.

In one specimen among thirteen, an addition to these structures came to light. On the right mantle, a chevron of tough tissue overlay the inner mantle lobe; its apex was at the junction of the spongy and tubular parts of the ridge, and its dorsal limb, about a millimeter long, ran anteriorly, parallel to the feeder vessel (a). The slightly shorter ventral limb was roughly symmetrical with the dorsal. On the left mantle edge, in opposing position, was a triangular pad of the same sort of tough tissue, apex dorsal, and base along the dorsal edge of the ridge. Protruding postero-ventrally from the posterior corner of the pad was a nubbin of tissue covering the ridge. This series of pads did not seem to be an accident of preservation, or pathological. We could not determine whether the pads were inflatable, although they seemed distinct from the ridges. Perhaps such pads would provide a crude lock to keep the ridges on the two halves of the mantle from slipping by each other during flexure of the "siphons."

Previous authors have not figured the pallial ridge and papillae accurately. SELENKA (1868), LEBKUCHNER (1933), and SAVELIEV (1958) depict no ridge and figure the entire posterior mantle edge with large, complex papillae. PELSENER (1891) draws the tubercles correctly but leaves



out the pallial ridge. Only DUVERNOY (1854) figured the mechanism correctly, but he said little about it in his treatise on the nervous system.

### Separation of Inhalent and Exhalent Water in Fossil Trigonians

Trigonian clams were among the most diverse and abundant animals of Mesozoic seas. The pallial ridge of the sole survivor does not represent the entire repertoire of mechanisms that trigonians evolved to separate incurrent and excurrent waters. A limited examination of specimens in the collection of fossil invertebrates at the Museum of Comparative Zoology, and of the literature yielded a set of solutions to this common problem. We cannot tell, of course, whether any fossil taxon possessed a pallial ridge, though the absence of other adaptations in several evident burrowers leads us to suspect that the ridge may not be a Tertiary innovation.

1. General shell form: The shell of *Neotrigonia* is subquadrate. Most fossil trigonians, as the name implies, are rather triangular with an extended posterior border (Figure 5). This extension produces no separation of incurrent and excurrent waters, but it does segregate the general area of intake and outflow from the rest of the shell. The extension of this area (into a posterior "tube" in extreme cases) must lead to deeper penetration and more efficient burrowing (Figure 5).

2. External ornamentation: Most fossil trigonians have distinctive, discrepant ornamentation (Figure 5). A prominent ridge, the marginal carina (Figure 5a), runs from the umbo to the postero-ventral border of the shell. This carina divides the shell into an anterior portion (the flank) and a posterior portion (the area) with very different patterns of ornamentation. The area is bounded ventrally by the marginal carina and dorsally, in most cases, by another ridge, the escutcheon carina (Figure 5b). It is often divided medially by a furrow running from the umbo to the middle of the posterior border. The literature on trigonians almost always describes these features without offering any functional interpretation. However, our theme—the necessity for separating influx and outflow channels in burrowing bivalves lacking mantle fusion—provides a ready explanation. The marginal carina marks the ventral border of the incurrent area, the escutcheon carina the dorsal edge of the excurrent flow. The medial furrow, when present, divides the posterior border into two lobes and produces separation, as in modern *Neotrigonia bednalli*.

3. Internal ridges and raised areas: In some trigonians, these external ridges and furrows have no internal expression; but this is not the usual situation. In almost all fossil shells, the escutcheon carina marks the beginning of a raised, internal shelf which corresponds to the entire escutcheon (postero-dorsal to the posterior tooth and to the posterior adductor scar). The shelves of both valves meet to form a strong dorsal border to the exhalent flow (Figure 6). This structure is especially evident on fossil *steinkerns* (internal molds) in which the width of the internal space is abruptly reduced to a ribbon along a line corresponding to the inception of the shelf.

Of much greater interest is the internal median ridge which often corresponds to the furrow marking separation of incurrent and excurrent water (Figures 6 and 7). Cox (1952) noted such a ridge in Triassic *Prorotrigonia* and Cretaceous *Pterotrigonia*. It is much more widespread. In a rather cursory examination, we found an internal ridge in four Jurassic (including the well-known *Laevitrigonia gibbosa*) and two Cretaceous species (including *Apiotrigonia sulcataria*), as well as in two species of *Pterotrigonia* (*Scabrotrigonia*)—the type *Pterotrigonia scabra*, and *Pterotrigonia eufaulensis* of the Upper Cretaceous Ripley Formation of Alabama. Many additional species have a broad, raised median area that must have produced some separation.

The internal ridge varies greatly in strength and extent among taxa. Yet it possesses a common trait with the pallial ridge of *Neotrigonia*: both structures are low and narrow at the posterior border, becoming higher and thicker towards the interior before declining again towards their anterior termination (Figures 2 and 6). The explanation is scarcely startling, but it does serve to emphasize an interesting morphological convergence for common function in non-homologous structures: right at the posterior margin, the shells are apposed and the ridge requires little height to attain contact with its opposite member; anteriorly, the shells diverge and the ridge, be it tissue or shell, must become higher in order to retain contact and continue to separate incurrent and excurrent waters.

It seems safe to conclude that some trigonians with median ridges lacked pallial ridges. In *Pterotrigonia scabra*, for example, the ridges are so high that they would prevent shell closure if they were to meet; in two articulated shells of this taxon, the median ridge of the left valve passes just ventral to that of the right valve as the shell closes.

In structural series of imperfectly siphonate clams, the ventral margin of the inhalent aperture is always last to form (YONGE, 1957). This is also true in modern trigoni-

ans: the exhalent current is bounded by the pallial ridge but the inhalent aperture, if formed at all, can only arise by local apposition of the mantle edges. Yet a few fossil trigonians also have an internal ridge or raised area corresponding to the ventral border of the inhalent area. This ridge is the internal expression of a groove running just posterior to the prominent marginal carina. Thus, a few fossil trigonians have three internal ridges or raised areas (the shelf corresponding to the escutcheon, the medial ridge and a ventral ridge corresponding to the groove of the marginal carina). These fossils probably possessed two complete "siphons" without any mantle fusion (Figure 7).

4. True siphons: NEWELL & CIRIACKS (1962) described the aberrant genus *Scaphellina* from the Permian of the western United States. It has a shallow pallial sinus and therefore, by common assumption, it also had fused mantles and true siphons. *Scaphellina* is not a true trigoniid; but belongs to the family Myophoriidae that most experts regard as ancestral to trigoniids.

Ordovician *Lyrodesma* is the first known bivalve with a pallial siphon (POJETA, 1971). On general shell form and some dental similarities, the Lyrodesmatidae (known only from *Lyrodesma* itself) have been linked to the much later Myophoriidae and hence to the ancestors of trigoniids. We doubt, however, that a shallow burrower, once it developed siphons, would abandon them for the range of imperfect solutions cited above. We prefer to regard the similarities as convergent. One could argue that *Lyrodesma* itself is a highly specialized offshoot of an unknown lyrodesmatid stock that eventually gave rise to trigonians, but at this point phyletic speculation enters the realm of fantasy.

Our catalogue of ingenious, yet imperfect, solutions raises a major principle in functional morphology. Often, we can best appreciate the importance of a key innovation by surveying the range of imperfect attempts to attain the same function with structures that cannot build the optimal form. In this case, true siphons cannot be constructed without mantle fusion; therefore, trigonians devised an array of solutions to the problem of separating incurrent from excurrent flow. They flourished very successfully for a time, but few could ultimately survive in a world increasingly dominated by better-designed siphonate forms. Likewise, at least three groups of reptiles (Triassic *Kuehneosaurus*, the pterosaurs and modern lizards of the genus *Draco*) have moved, with greater or less success, in the direction of flight; yet only the group that developed key characters of feathers and homeothermy evolved into birds. If the pelycosaurian sail did function in heat regulation (we suspect, with DAVITASHVILI (1961),

that sexual display was its primary purpose), then the line that ultimately did give rise to mammals performed some prior and less successful experiments in homeothermy.

Is it possible, however, that the more general ability to operate a complex hydraulic mechanism at the posterior mantle border might extend beyond the advantages of a pallial ridge separating incurrent from excurrent flow. The freshwater unionids are the closest living relatives of trigoniids. Several species of *Lampsilis* have evolved one of the most striking and peculiar adaptations of the entire animal kingdom: an extension of the posterior mantle, looking for all the world like a little fish and even capable of a flapping movement which simulates swimming (KRAEMER, 1970). Since the glochidia larvae of unionids must attach to fish, this mantle flap apparently functions as a lure. The flapping movement is nervous and muscular in origin, but the "fish" is inflated hydraulically. The "fish" is located just ventral to the incurrent siphon, but it is formed by extensions of the inner layers of mature female's anal and branchial siphon edges. We are not, of course, suggesting that the pallial ridge of *Neotrigonia* be homologized with the "fish" of *Lampsilis*; yet it may not be completely without interest that two related groups have developed such complex hydraulic mechanisms at their posterior mantle borders.

### Typology of Separation in Modern Bivalves

An account of the various ways in which modern bivalves effect a separation of incurrent and excurrent water emphasizes the significance of the pallial ridge in *Neotrigonia*; for this ridge represents the only morphological structure for producing "siphons" in forms without mantle fusion. We present this account as a sequence moving towards increasingly greater degrees of mantle fusion (partly taken from YONGE, 1957). This sequence is neither evolutionary nor even a series of increasingly better designs. All stages represent good designs for certain habitats (though the key innovation of fusion marks an evolutionary advance of first importance in the history of bivalves).

#### A. Unfused Mantle Margins

1. Broad and changing areas separated by apposition. The ostreids *Malleus* (YONGE, 1968) and *Crassostrea* (NELSON, 1938), by local apposition of their pallial curtains, separate broad areas of incurrent and excurrent flow. *Pedum spondyloideum*, a scallop living in crevices of reef-building corals, maintains a "somewhat movable boundary between the inhalent and exhalent openings"